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Reproductive ecology of a deep-water scleractinian coral, *Oculina varicosa*, from the southeast Florida shelf

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Abstract

The Ivory Tree Coral *Oculina varicosa* forms extensive reefs of azooxanthellate colonies at depths of 70–100 m along the edge of the Florida Hatteras slope. Healthy reefs support invertebrate and fish communities as diverse as those of tropical coral reefs, and are a critical spawning habitat for a number of commercial fisheries species. A 3-year study of reproduction and larval development revealed that *O. varicosa* is a gonochoristic broadcast spawning species, with small eggs (<100 μm) and high fecundity values. The gametogenic cycle begins in the early summer and spawning occurs during late summer and fall, with no obvious relationship to lunar or tidal phase. Planulae are small (approximately 160 μm), active swimmers that can withstand a wide range of temperatures and that settle approximately 21 days after spawning. Given the hydrodynamics of the Florida Hatteras shelf, larvae not only have the potential to be transported between the deep reef tracts, but may also contribute to nearshore zooxanthellate populations during summer upwelling events.

Keywords: Coral; Reproduction; Ahermatypic; Reef; Marine reserve; USA; Florida; Fort Pierce (27°32.54 N, 79°58.73 W)

1. Introduction

1.1. *Oculina*, distribution and biology

Oculina varicosa (Leseur 1820) is an ahermatypic branching scleractinian coral that occurs at depths between 3 and 100 m. In deep water, it forms bushes of fragile colonies, creating continuous tracts of reef on the slopes and tops of pinnacles, similar in structure to deep-water *Lophelia* reefs (Reed, 1992, 2000). These unique deep-water *Oculina* reefs are known to exist only on the shelf edge off eastern Florida, and stretch over 90 nautical miles (167 km) from Fort Pierce to Daytona (Macintyre and Milliman, 1970; Avent et al., 1977; Reed, 1980). The same species also inhabits shallow-water limestone ledges (3–30 m) as a different morphological variant. Colonies of the shallow-water phenotype are much smaller (<30 cm) and have thicker branches than the deeper forms; they also contain zooxanthellae, giving the coral a golden-brown coloration, whereas the deep populations are normally azooxanthellate.

The deep *Oculina* biotherms are the only known monospecific banks of coral that occur on the

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North American continental shelf (<200 m depth), although similar bioherms of *Lophelia pertusa* and *Enallopsammia profunda* exist in deeper waters at the base of the Florida Hatteras slope and the Blake Plateau (Reed, 2000). All of these deep-water 'reef-building' corals have a similar growth pattern, which is unlike that of typical shallow water species. As the colony increases in diameter, the tangled outer branches block water flow to the core of the colony, and this stagnation causes the inner branches to die. Bioerosional processes weaken the dead coral branches, which eventually break and the colony falls apart. The outer living branches continue to grow, and new recruits may also colonize the exposed dead core. As this process continues over thousands of years, these mounds and pinnacles can reach tens of meters in height, with the live coral forming a cover over the unconsolidated dead coral debris below.

The deep shelf-edge *Oculina* reefs form natural spawning grounds for commercially important populations of gag (*Mycteroperca microlepis*) and scamp (*M. phenax*) grouper. They also serve as nursery grounds for juvenile snowy grouper (*Epinephelus niveatus*), and feeding grounds for these and many other commercial fish species (Gilmore and Jones, 1991; Koenig et al., 2000). The deep-water reefs also support very rich communities of invertebrates; faunal diversity on the *Oculina* banks is equivalent to that of many shallow tropical reefs. Over 20,000 individual invertebrates were found living among branches of 42 small *Oculina* colonies, yielding more than 350 different species (Reed, 1992; Reed and Hoskin, 1987; Reed and Mikkelson, 1987; Koenig et al., 2000), many of which are important food sources for animals at higher trophic levels.

In 1984, the South Atlantic Fishery Management Council designated 92 square nautical miles of the deep *O. varicosa* banks as a Habitat of Particular Concern (HAPC) because of their value as important fish habitat. Mobile fishing gear and anchoring (1995) were prohibited to protect the

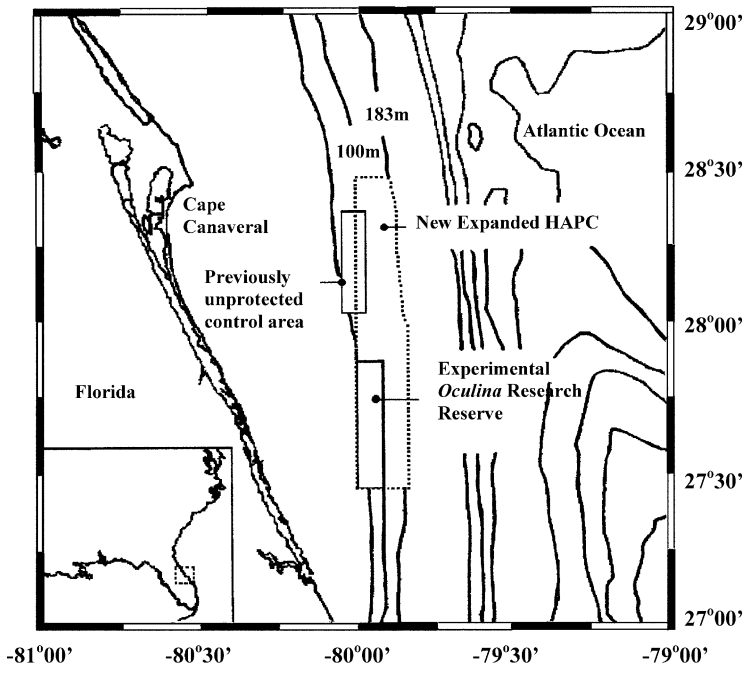

Fig. 1. Map of the *Oculina* habitat area of particular concern (OHAPC). The recently expanded area (July 2001) is represented as a dashed rectangle. The solid boxes delineate the Experimental *Oculina* Research Reserve, and previously unprotected "control" areas.

delicate *Oculina* thickets. In 1994, the HAPC was closed to all bottom fishing for 10 years. This area was designated the Experimental *Oculina* Research Reserve or EORR. In 2000, the HAPC area was extended to encompass $\sim 300\,nm^2$ of the banks, which includes most of the known areas of the *Oculina* reefs (Fig. 1). Parts of the *Oculina* banks have been extensively damaged, but the exact causes of the damage are open to speculation. Natural processes, disease, unfavorable environmental conditions and destructive fishing practices may all have been contributing factors.

Despite the value of *Oculina* reefs as valuable habitat, the reproductive biology of the coral has been poorly studied. Understanding the life history of the coral would be helpful when devising restoration strategies. For example, a species with low fecundity, poor dispersal and a low recruitment rate is unlikely to rapidly re-colonize a denuded area. In contrast a highly fecund, dispersive species with good settlement rates may only need adequate substrate for re-colonization to occur. The objective of this research was to provide information on ecologically relevant aspects of reproduction, such as duration of breeding season, fecundity and potential larval supply that may be useful in efforts to restore the damaged areas.

2. Methods

2.1. Sampling, processing and maintenance of adult O. varicosa colonies

Samples of *O. varicosa* were collected on eight separate cruises between March 1998 and September 2001. Twelve sets of samples were taken in total, all from depths between 80 and 100 m. Six collections were made at Jeff's Reef (27°32.54′N, 79°58.73′W), using either the National Marine Fisheries Service Phantom ROV (February 1999), the Johnson Sea Link research submersible (June 1999), the Harbor Branch Oceanographic Institution submersible recovery ROV (April and July 2000), or the Clelia research submersible (March 2001, September 2001). Two collections were made (March 1998, September 2000) outside the HAPC at a site off Cape Canaveral, (28°29.82′N, 80°01.24′W), using a small (1.5 m swath) trawl. One set of samples was collected from a site called the Steeple (27°43.60′N, 79°58.759′W), in February 1999, using the NMFS Phantom ROV. A set of samples was also collected from Eau Gallie (28°08.6′N, 79°59.5′W), Sebastian Pinnacles (27°50.974′N, 79°57.698′W) and Chapman's Reef (27°36.4′N, 79°58.4′W) in September 2001 using the research submersible Clelia. During each collection, samples were taken from several (5–12) different healthy colonies. Small pieces of each branch were preserved immediately for histological analysis in 10% buffered formalin During periods of potential larval release (as indicated by histological sampling), larger branches were placed in aerated coolers for transport to the laboratory, where they were transferred to recirculating seawater tanks at 16°C. The tanks were kept in the dark to prevent algal growth (light deprivation had no visible adverse affect on these azooxanthellate colonies), and the corals were fed every third day with freshly hatched nauplii of the brine shrimp *Artemia franciscana*.

2.2. Determination of reproductive strategy and gametogenic cycles

For histological examination, polyps at the base of the sample branches were used, as the small polyps at the branch tips were potentially non-reproductive (Rinkevich and Loya, 1987). After decalcification in 10% hydrochloric acid for 6–10 h, polyps were dehydrated through a series of ethanol concentrations, embedded in paraffin wax, cut into 8 μm sections, and stained using Mayer's Haematoxylin/Eosin B staining techniques. Images of oocytes were taken using an Optronics digital camera attached to an Olympus BX50 compound microscope. The slides were used to determine whether the corals are brooders or broadcast spawners, and gonochoristic or hermaphroditic, as well for description of reproductive cycles.

The area of each oocyte was measured and recorded using Image Tool (UTHSCSA) image analysis software. Oocyte 'feret' diameter was calculated, which estimates the diameter of a hypothetical circle with the same area as the object

measured:

$$\text{Feret diameter} = \sqrt{\frac{4 \times \text{area}}{\pi}}.$$

Information on oocyte feret diameter and size-frequency distribution was used to infer the timing of the gametogenic cycle. Three female colonies were used for each sampling date, (except for July 1999, where only one female was available) and a total of 50 oocytes were measured from 2–3 individuals per colony. Oocyte size-frequency distributions were then generated using the oocyte feret diameter data. The male histological sections were examined and the percentage of gonads containing mature sperm was calculated for 20 mesenteries per colony at each sampling date. To facilitate comparisons of maturity between males and females, the percentage of gonads containing mature oocytes was also calculated for 20 mesenteries per colony. Oocytes with a diameter of 60 μm (which represents lower size limit of mature oocytes for these populations) or above were designated 'mature''. Analysis of variance was used to test for significant ($p < 0.05$) intra-month differences in female data sets. A paired *t*-test on arcsin transformed data was used to compare the percentage maturity of females and males across the reproductive season.

2.3. Fecundity

Samples collected during September of 2000 and 2001 were used for fecundity analysis. Samples were fixed in 10% seawater-buffered formalin solution for 24 h and then washed in distilled water and transferred to 30% ethanol for dissection, using fine forceps and needles under a dissecting microscope. The polyp length and number of eggs per polyp were recorded for five polyps from each of five female colonies for each year. Regression analysis was used to determine whether fecundity increases as a function of increasing polyp length. Inter-colony and inter-annual variation was tested using one-way analysis of variance and Student's two-tailed *t*-test, respectively ($p < 0.05$).

The number of polyps per cm^2 of skeletal surface area (SSA) was estimated to facilitate comparison of *O. varicosa* fecundity with that of other scleractinian species in the literature. A piece of aluminum foil was cut to a known size (either 25 or 12.5 cm^2), and wrapped around the branches of 12 samples of *Oculina* skeleton. The number of polyps covered by the foil was counted and the average number of polyps per cm^2 of surface skeletal area was then calculated.

2.4. Spawning and larval culture

During potential spawning periods, small samples of coral from 8 to 15 different colonies were kept in a 2-l glass bowl containing filtered (20 μm) seawater, which was changed daily. When spawning was observed sperm and eggs were removed immediately and transferred to 200 ml finger bowls containing 0.45-μm-filtered seawater for fertilization and embryogenesis. Fully developed planulae were placed in 1-l glass culture jars containing 0.45-μm-filtered seawater and incubated at 20°C. If spawning occurred overnight, larvae were removed from the bowl and transferred to culture jars the following morning. The larval cultures were stocked at a density of approximately 5 larvae/ml, and 75% of the water was exchanged every 2 days to keep the cultures clean. The larvae were used for behavioral observation, physiological experiments, and to determine duration of larval life.

2.5. Effect of temperature on larval swimming speed

Larvae from a single 9-day old culture were placed in 40-ml scintillation vials at a stocking density of 5 larvae/ml. The experimental temperatures used were 5°C, 10°C, 15°C, 20°C, 25°C, 30°C and 35°C, with three replicate vials per treatment. The larvae were gradually acclimated to the experimental temperatures from ambient culture temperature (20°C). After 6 h of incubation, the larvae from each vial were placed in a small Petri dish under an Olympus SZH10 dissecting microscope at 50× magnification. A video camera was connected to the microscope and footage of larval swimming was recorded for 2 min onto Hi-8 videotape. A scale was included

with each recording for future assessment of distance. To measure swimming speed, a sheet of acetate was taped to the screen of a video monitor (29 cm screen), and for each sample the distance traveled by 20 individual larvae was recorded at 2-s intervals until they disappeared from view. The swimming speed of each larva was then calculated using the average distance traveled during these intervals.

3. Results

3.1. Reproductive strategy and gametogenic cycles

O. varicosa was found to be a gonochoristic broadcast spawning species with no indication of brooding or asexual planula production. The reproductive tissues of scleractinians are not contained within a true organ, but for ease of description, they will henceforth be referred to as gonads. In *O. varicosa* the gonads are situated within the mesenteries, closely associated with the mesenterial filament. *O. varicosa* has 12 pairs of mesenteries, with one member of each pair usually larger than the other. There appears to be just one large area of reproductive tissue per mesentery, which expands as the reproductive season proceeds. The oocytes are compressed, irregular-shaped discs whilst in the mesentery, but become spherical just prior to expulsion, or shortly thereafter. The testes have many lobes, giving the impression of multiple gonads in histological sections of males. Small genital pores are visible in the mesentery wall of ripe adults, which may allow passage of gametes into the gastrovascular cavity prior to spawning.

Histological sections of polyps collected in March 1998 and February 1999 showed no indication of reproductive activity. In June 1999, small oocytes (mean 41.8 μm, ±7.2) in the early stages of vitellogenesis were observed. Larger oocytes were observed in July 1999 (56.6 μm, ±0) and 2000 (46.4 μm, ±4.7), and a small spawning event occurred in the laboratory on August 9, 2000. Samples collected in September 2000 and 2001 contained the largest oocytes (69.4 μm, ±7.9 and 61.9 μm, ±7.9, respectively)

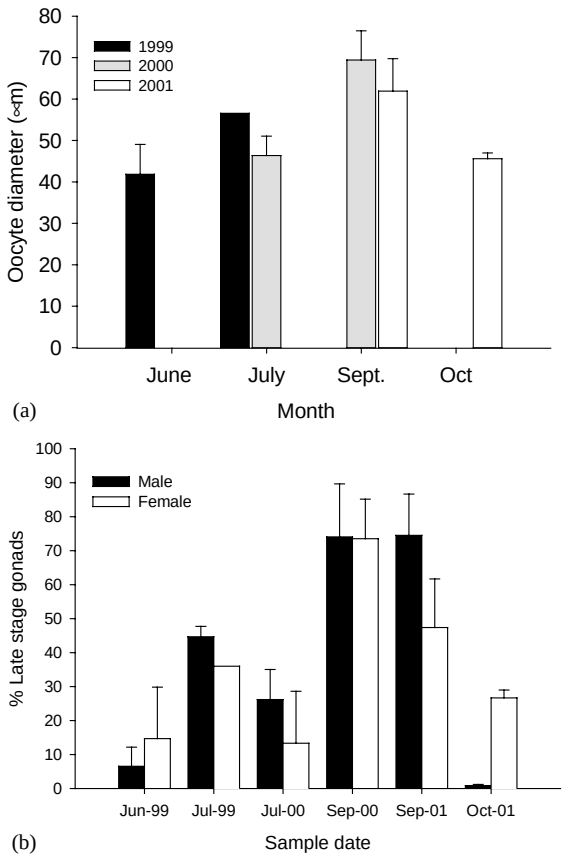

Fig. 2. (a) Oocyte development over time for deep-water *Oculina* colonies. Fifty oocytes were measured from three different colonies per sample date, except July 1999 when only one female colony was available. Error bars represent standard deviation from the mean of the three colonies. (b) Percentage of gametogenic material in the late stages of development, i.e. male gonads with heavily stained sperm and females with oocytes >60 μm in diameter. Twenty mesenteries were scored for gonad maturity from each of three different male and female colonies per sample date. Error bars represent standard deviation from the mean of the three male and female colonies.

(Fig. 2A). A large spawning event was observed by samples collected on the night of September 9, 2000 and samples collected in September 2001 spawned on the night of September 7; however, fewer than 1000 eggs were released during this event. The histological data show a decrease in mean oocyte diameter between September and October 2001. A small number of late stage oocytes and some small oocytes (45.5 μm, ±1.4)

were present in October. These gonads did not appear to be undergoing a second gametogenic cycle as the eggs were few and poorly organized within the gonad area, rather they appeared to be remnant oocytes from the previous gametogenic cycle. The percentage of mature male gonads was low in late June 1999 (6.57%), but increased rapidly in July 1999 to 44% (Fig. 2B). In 2000, development was slower, but by September of both 2000 and 2001, 74% of the male mesenteries contained ripe testes. The percentage of mature testes present in the mesenteries fell considerably in October to less than 1%. A paired t-test on arcsin transformed data showed no significant difference between percentage maturity of males and females across the reproductive season ($t = 0.34$, $p = 0.75$). Gametogenesis therefore increased synchronously between males and females (Fig. 2B).

Samples were analyzed for inter-colony variation in oocyte diameter within sampling date, using one-way analysis of variance. When the data failed to meet the conditions of normality and homogeneity of variance, an ANOVA on ranks was performed and the H-statistic is presented. All sample months for 1999, 2000 and 2001 showed a significant difference between colonies ($p < 0.001$) (Table 1), except for October 2001 ($H = 0.81$, $p = 0.71$), indicating a lack of synchrony between colonies throughout the gametogenic cycle.

Table 1
Analysis of variance of oocyte feret diameter from colonies within sample months

Sample month	Test statistic	P
June 1999	$F = 11.50$	0.00*
July 1999	N/A	0.00*
July 2000	$H = 10.31$	0.01*
Sept 2000	$F = 7.89$	0.00*
Sept 2001	$F = 13.42$	0.00*
Oct 2001	$H = 0.81$	0.66

*Significance level $p < 0.05$; an asterisk denotes those months where oocyte size differed significantly between colonies. Except where otherwise labeled, all the test statistics are one-way ANOVA (F). Those data sets that failed tests for normality and/or homogeneity of variance were analyzed using ANOVA on ranks (H).

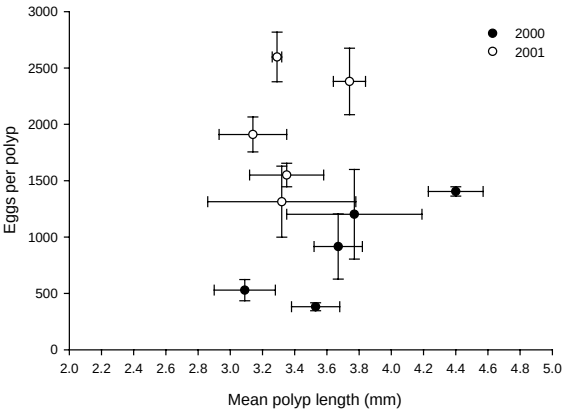

Fig. 3. The relationship between fecundity (eggs per polyp) and polyp length for *O. varicosa* samples collected in September 2000 and 2001. Y error bars represent the standard deviation from the mean fecundity of 5 polyps per colony. X error bars represent standard deviation from the mean polyp length for 5 colonies per year.

3.2. Fecundity

The relationship between number of eggs per polyp and mean polyp length ($n = 5$ colonies) for samples collected in 2000 and 2001, are represented in Fig. 3. Regression analysis shows a non-significant relationship between fecundity and polyp length for 2000 (r^2: 0.688, $F = 7.95$, $p = 0.07$) and 2001 (r^2 : 0.1, $F = 0.35$, $p = 0.6$). Fecundity was standardized to represent eggs per mm of polyp length, and a one-way ANOVA showed a significant difference in fecundity between deep-water colonies collected in 2000 ($F = 7.028$, $p = 0.006$) and 2001 ($F = 21.80$, $p = 0.001$). The results of an unpaired two-tailed t-test show a significant inter-annual difference in fecundity of deep-water colonies from 2000 and 2001 ($t = -3.5$, $p = 0.01$). To facilitate comparisons with data in the literature, fecundity data were translated into number of eggs per cm^2 of SSA. This was calculated by multiplying eggs per polyp by 2.39, the mean number of polyps per cm^2 of SSA. Polyps from the branch tips were not included in this fecundity measurement; however, both male and female polyps as small as 2 mm from the branch tips contained testes or vitellogenic oocytes.

3.3. Spawning and larval observations

Spawning of deep-water *O. varicosa* was first observed at 11 p.m. on August 9, 2000, but fewer than 1000 eggs were released. The samples had been collected during a cruise in July and maintained in static aquaria in the laboratory. The largest spawning event occurred during a cruise in September 2000 when corals were collected and held in a large aerated barrel on the deck of the ship. The samples were checked at 23:30 on the night of September 9. At 08:30 the following morning, early stage planulae were swimming at the surface of the water in the barrel. The corals had therefore spawned and the gametes had developed into larvae during the time between observations. The third spawning event occurred at 10 p.m. on September 7, 2001. The spawning events all occurred late at night, but showed no obvious correlation with tidal or lunar phase. Male colonies spawned before the females in each observed event, releasing sperm in quick bursts through the mouth of the polyp. Females also release eggs through the mouth in bursts similar to those of the males. The eggs are approximately 100 μm in diameter, opaque white in color and negatively buoyant. Each male polyp released sperm intermittently for 30–45 min and the corals continued to spawn over a period of several hours.

Embryogenesis occurred over a period of approximately 9 h at 25°C, giving rise to small (160 μm) well-ciliated, azooxanthellate planulae. Fig. 4 shows a scanning electron micrograph of a newly developed planula; the larvae were elongated anterior–posteriorly, with the oral pole slightly wider than the aboral pole. Active nematocysts scattered between the epithelial cilia fired rapidly when the larvae become trapped beneath the glass cover slip of a microscope slide. After approximately 1 week, a long ciliated apical tuft appeared on the aboral pole. This apical tuft was lost just prior to settlement.

Ciliated planulae swam immediately to the surface of the water, even when maintained in the dark and observed under red light, and remained there for between 18 and 24 h. The larvae swam rapidly with the aboral pole forward, in a spiral fashion rotating clockwise around the longitudinal axis. Larvae swam actively in the culture containers for 1–2 weeks, after which time they began to exhibit benthic-probing or creeping behavior. The larvae were very plastic in their morphology and frequently contracted or bent, especially during benthic probing activity. Once the larvae became competent, they were divided into groups and offered a variety of settlement cues from extracts of coralline algae (Heyward and Negri, 1999), to dead coral skeleton, glass slides and limestone rubble. The results of these experiments were inconclusive and those larvae that were observed to settle (between 21 and 27 days) did so on the sides of the culture containers rather than the proffered substrates, and subsequently died as a result of bio-fouling. Some of the larvae continued swimming for up to 42 days, after which time, the cultures were terminated.

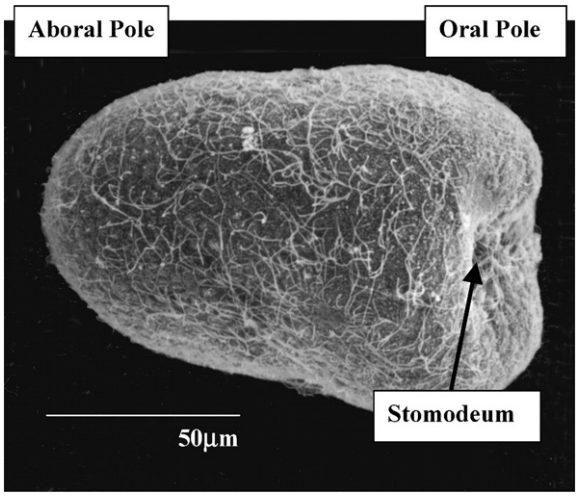

Fig. 4. Scanning electron micrograph (× 200) of an *O. varicosa* planula (age 24 h)

3.4. Effect of temperature on larval swimming speed

Swimming speed is temperature dependent (Fig. 5) ranging from an average of 1.9 mm s^{-1} at 25°C, to 0.59 and 0.66 mm s^{-1} at the experimental extremes of 5°C and 35°C, respectively. A one-way analysis of variance shows a significant difference between the temperatures ($F = 82.67$,

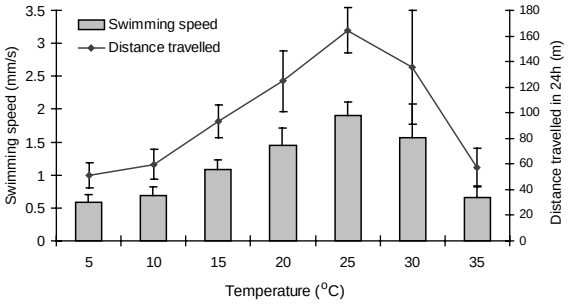

Fig. 5. Effect of temperature on swimming speed of deep-water *O. varicosa* larvae and estimated distance travelled after 24 h of vertical migration at different temperatures. Error bars represent standard deviation from the mean swimming speed of three replicates (20 larvae per replicate) at each temperature.

$p<0.001$). The additional plot in Fig. 5 shows the estimated position of the larvae in the water column after 24 h of vertical migration, after which time, larvae at all temperatures except the most extreme would be capable of reaching the surface from 80 m depth.

4. Discussion

4.1. Gametogenesis

There is evidence for exogenous control of reproduction in a variety of marine invertebrates, in terms of both proximal (immediate) and ultimate (evolutionary) cues (Giese and Pearse, 1974). These include sea temperature, day length, salinity, supply, lunar phase, tidal cycles and daily light/dark cycles (Giese and Pearse, 1974; Himmelman, 1980; Babcock et al., 1986; Yankson, 1986; Harrison and Wallace, 1990; Johnson, 1992; Sasaki and Shepherd, 1995; Hardege and Bentley, 1997). In corals the evidence is correlative only and specific regulatory mechanisms have yet to be determined. Seasonal change in sea temperature is frequently cited as an important environmental factor that controls gametogenic cycles and planular release in scleractinian corals (Szmant-Froelich et al., 1980; Kojis and Quinn, 1981; Tranter et al., 1982; Fadlallah, 1985; Stoddardt and Black, 1985; Babcock et al., 1986; Harrison and Wallace, 1990). Simpson (1985), however, found that gametogenesis and mass spawning periods differ between populations of the same species on the east and west coasts of Australia, despite similar seasonal temperature regimes. This implies that factors other than temperature also influence reproductive cycles.

Oculina populations are periodically subjected to influxes of cold water that is forced up over the shelf edge by meanders of the Florida Current, and which may confound seasonal temperature trends. Other environmental factors such as light levels, sediment load and current regime are also highly unpredictable. Kojis (1986) suggested that changes in day length provide more consistent cues than temperature for corals living in shallow reef flats; for example, oogenesis in *Acropora palifera* colonies may be initiated by increasing day length, minimum or maximum day lengths or both. It is possible that gametogenesis of *O. varicosa* is also entrained by changes in day length as this varies predictably from year to year regardless of temperature, lunar/tidal cycles or turbidity. At a latitude of 28°N the number of daylight hours undergoes its greatest change increases between April and May, when gametogenesis is initiated.

Gametogenic cycles in broadcast spawning coral species are all synchronous to some degree (Fadlallah, 1983) as is necessary to ensure that the gametes are fertilized. Many tropical hermaphroditic species release gametes according to strict lunar schedules over a short period of time every year (Kojis and Quinn 1981, 1982a b; Harrison et al., 1984; Simpson, 1985; Babcock et al., 1986; Harrison and Wallace, 1990). Gonochoristic broadcast spawners tend to have longer reproductive seasons and less tightly synchronized spawning periods than their hermaphroditic counterparts, with gamete release occurring over a number of weeks (Minchin, 1993; Harrison and Wallace, 1990). Spawning events by *O. varicosa* colonies occurred up to 31 days apart in 2000, and colonies of *O. varicosa* exhibit asynchronous gametogenesis, as indicated by the high levels of variance in late stage gonads during September (Fig. 2B). These results may reflect an extended spawning period in *O. varicosa* populations. Asynchrony of gametogenesis and spawning provides the population with some security against

releasing gametes into unfavorable water conditions or into currents, which may carry them away from suitable settlement habitat. The data for *O. varisoca* also indicate that males and females exhibit concurrent initiation of gametogenesis and maturation.

4.2. Fecundity

Fecundity is usually expressed in corals as the number of eggs or planulae produced per polyp. Since only female reproduction is measured however, fecundity underestimates the reproductive effort of the total population. Harrison and Wallace (1990) combined fecundity data from 32 species of scleractinian and they discovered an inverse relationship between fecundity and egg size. Those species with eggs of $<250\,\mu m$ in diameter contained between 1000 and 10,000 eggs cm^{-2} of SSA. *O. varicosa* falls within this fecundity range, with a mean of 2115 (± 1034) eggs cm^{-2} of SSA for 2000 and 4693 (± 1301) for 2001. The large inter-annual difference in fecundity of *O. varicosa* is probably a reflection of the high environmental variability of the shelf-edge habitat, resulting in variable food availability and energy demands for competing processes. Since the samples were collected during the spawning season, some of the variation observed may be due to egg release prior to sampling in some of the females.

4.3. Larvae

In laboratory cultures, *O. varicosa* larvae invariably swam towards the water surface upon formation of ciliary bands, and remained there for several hours, after which they began to swim throughout the water column or became demersal. This behavior has been reported in planulae from other species in the laboratory (Atoda, 1953; Lewis, 1974; Szmant-Froelich et al., 1985), and has been attributed to changing phototactic or geotactic responses. This behavior was observed in *O. varicosa* larvae, even when embryos were kept in the dark and the resulting larvae were observed under red light, which implies a negative geotactic rather than a phototactic response. For oceanic plankton, there is a risk of predation and unfavorable transport associated with the upper part of the water column. Conversely, staying near the reef also presents the risk of being consumed by adult corals or other benthic predators. The larvae may avoid the hazards of the reef by moving up in the water column, but ultimately have to return to the benthos to settle. Larval swimming and settling behaviours accounted for much of the adult distribution of the leaf coral *Agaricia humilis* in Bonaire (Raimondi and Morse, 2000).

Many coral larvae are lecithotrophic, but small larvae without maternal energy stores need exogenous food to survive for extended periods in the plankton. Tranter et al. (1982) documented feeding by larvae of the cold water scleractinian, *Caryophylla smithii*, which are azooxanthellate and similar in size (130 μm) to larvae of *O. varicosa* (160 μm). Larvae of *C. smithii* feed by trailing mucous strings from the oral pole, which entangle food particles and are ingested into the gastric cavity. Whether *O. varicosa* larvae feed on exogenous food particles is still undetermined, but warrants further investigation.

The deep *Oculina* populations are predominantly found at depths of 70–100 m between 27°30′N and 28°30′N on the edge of the Florida Hatteras slope. Studies of shelf hydrodynamics (Smith, 1981, 1983, 1987) show that periodic upwelling events occur throughout the year, forcing cold nutrient-rich oceanic water up over the shelf edge. Temperature can have a significant effect on mortality and metamorphosis in coral larvae (Edmunds et al., 2001); however, the investigation into the effect of temperature on larval swimming speed shows that *O. varicosa* larvae can survive the temperature extremes that occur at the reef during the spawning season. The results of this experiment also show that larval swimming speed decreases as temperature is reduced, which can be explained by the combined effects of higher water viscosity and slower metabolic rate at lower water temperatures. Although ocean currents primarily control large-scale larval transport, impaired swimming speed may reduce the ability of the larvae to control their vertical position in the water column.

The strongest cross-shelf transport events occur during the late summer when the *Oculina* are spawning (Smith, 1983). It is unclear how much of the recruitment onto the nearshore reefs comes from deep-water larvae, but the mechanism for transport exists in these upwelling events. The upwelling water is less likely to be forced close to shore at Cape Canaveral where the shelf is wide, than further South in Fort Pierce where the shelf is quite narrow. Since the along-shelf water movement is dominated by the Florida Current, the prevailing flow is in a northerly direction; however, there are occasional direction reversals that can potentially transport larvae north or south between both deep and shallow reef tracts. During the spawning season in 2001 current meter data from Jeff's Reef show highly variable current speed and direction. If larvae swim upwards, as indicated by their behavior in the laboratory, they may encounter the Florida current, which has strong Northerly flow and forms complex gyres. Some gametes may be spawned into currents that transport the larvae to suitable settlement sites, whereas others may be carried to unsuitable habitat or out to sea and lost. A three-dimensional hydrodynamic model of the shelf and further information on larval behavior are required before informed estimates of larval dispersal can be made.

5. Conclusions

O. varicosa is a broadcast spawning species with high-colony fecundity and a long-lived planktonic larval stage. The larvae are active swimmers and can adjust their position in the water column; they are also able to tolerate the wide range of temperatures that may occur in the deep reef habitat. These characteristics are conducive to recolonization of the deep *Oculina* habitat, but there is little information available on other important processes such as larval supply, recruitment rates and post recruitment survival. Unfavorable larval transport, insufficient suitable substrate, low natural recruitment rates, and continued disturbance from illegal fishing activity may all impede reef regeneration. Between 1996 and 2001, large concrete modules were deployed in damaged areas of the *Oculina* banks as part of a restoration effort, but to date very little coral recruitment has been observed. Further research on *Oculina* larval settlement and a three-dimensional model of the complex hydrodynamic regime of the Florida shelf would enable prediction of larval transport and recruitment within and between *Oculina* populations.

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References

Atoda, K., 1953. Larva and postlarval development of the reef building corals. Science Reports of the Tohoku University 4 (20), 105–121.

Avent, R.M., King, M.E., Gore, R.H., 1977. Topographic and faunal studies of shelf edge prominence off the Central Eastern Florida Coast. Internationale Revue der Gesamten Hydrobiologie 62 (2), 185–208.

Babcock, R.C., Bull, G.D., Harrison, P.L., Heyward, A.J., Oliver, J.K., Wallace C, .C., Wills, B.L., 1986. Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Marine Biology 90, 379–394.

Edmunds, P.J., Gates, R.D., Gleason, G.F., 2001. The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. Marine Biology 139 (5), 981–989.

Fadlallah, Y.H., 1983. Sexual reproduction, development and larval biology of scleractinian corals. A review. Coral Reefs 2, 129–150.

Fadlallah, Y.H., 1985. Reproduction in the coral *Pocillopora verrucosa* on the reefs adjacent to the industrial city of Yanbu, Red Sea, Saudi Arabia. Proceedings of the Fifth International Coral Reef Congress, Vol. 4, Tahiti, 1985, pp. 313–318.

Giese, A.C., Pearse, J.S., 1974. Introduction. In: Giese, A.C., Pearse, J.S. (Eds.), Reproduction of Marine Invertebrates. Acoelomate and Pseudocoelomate Metazoans, Vol. 1. Academic Press, New York, pp. 1–49.

Gilmore, R.G., Jones, R.S., 1992. Color variation and associated behavior in the epeinepheline groupes *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* (Jordan and Swain). Bulletin of Marine Science 51, 83–103.

Hardege, J.D., Bentley, M.G., 1997. Spawning synchrony in *Arenicola marina*: evidence for sex pheromonal control. Proceedings of the Royal Society of London Series B 264 (1384), 1041–1047.

Harrison, P.L, Babcock, R.C., Bull, G.D., Oliver, J.K., Wallace, C.C., Willis, B.L., 1984. Mass spawning in tropical reef corals. Science 223, 1186–1189.

Harrison, P.L., Wallace, C.C., 1990. Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky, Z. (Ed.), Ecosystems of the World., Vol. 25. Elsevier, New York, pp. 133–207.

Heyward, A.J., Negri, A.P., 1999. Natural inducers for coral larval metamorphosis. Coral Reefs 18 (3), 273–279.

Himmelman, J.H., 1980. Synchronization of spawning in marine invertebrates. In: Clark Jr., W.H., Adams, T.S. (Eds.), Advances in Invertebrate Reproduction. Elsevier, North-Holland, New York, pp. 3–19.

Johnson, K.G., 1992. Synchronous planulation of *Mancina areolata* (scleractinia) with lunar periodicity. Marine Ecology Progress Series 87, 265–273.

Koenig, C.C., Coleman, F.C., Grimes, C.B., Fitzhugh, G.R., Scanlon, K.M., Gledhill, C.T., Grace, M., 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. Bulletin of Marine Science 66 (3), 593–616.

Kojis, B.L., 1986. Sexual reproduction in *Acropora* (*Isopora*) (Coelenterata: Scleractinia). II. Latitudinal variation in *A. Palifera* from the Great Barrier Reef and Papua New Guinea. Marine Biology 91, 311–318.

Kojis, B.L., Quinn, N.J., 1981. Aspects of sexual reproduction and larval development in the shallow water hermatypic coral *Goniastera australensis* (Edwards and Haime, 1857). Bulletin of Marine Science 31, 558–573.

Kojis, B.L., Quinn, N.J., 1982a. Reproductive strategies of four species of Porites (Scleractinia). Proceedings of the Fourth International Coral Reef Symposium, Manila, Phillipines, Vol. 2, pp. 145–151.

Kojis, B.L., Quinn, N.J., 1982b. Reproduction of two Faviid corals (Coelenterata: Scleractinia). Marine Ecology—Progress Series 8, 251–255.

Lewis, J.B., 1974. The settlement behavior of the planula larvae of the hermatypic coral *Favia fragrum* (Esper). Journal of Experimental Marine Ecology 15, 165–172.

Macintyre, I.G., Milliman, J.D., 1970. Physiographic features on the outer shelf and upper continental slope, Atlantic continental margin, Southeastern United States. Bulletin of the American Geological Society 81, 2577–2598.

Minchin, D., 1993. Multiple species, mass spawning events in an Irish Sea Lough: the effects of temperature on spawning and recruitment of invertebrates. Invertebrate Reproduction Development 22, 229–238.

Raimondi, P.T., Morse, A.N.C., 2000. The consequences of complex larval behavoir in a coral. Ecology 81 (11), 3193–3211.

Reed, J., 1980. Distribution and structure of deep-water *Oculina varicosa* coral reefs off central eastern Florida. Bulletin of Marine Science 30 (3), 667–677.

Reed, J., 1992. Submersible studies of deep-water *Oculina* and *Lophelia* coral banks off the South-eastern USA. Proceedings of the American Academy of Underwater Sciences 12th Annual Scientific Diving Symposium, Wilmington, NC.

Reed, J., 2000. Comparison of deep water *Oculina* and *Lophelia* coral banks and lithoherms off southeastern Florida. In: Proceedings of the First International Symposium on Deep Sea Corals. Science and Conservation of Deep Sea Corals, Halifax, Nova Scotia, abstract only.

Reed, J.K., Hoskin, C.M., 1987. Biological and geological processes at the shelf edge investigated with submersibles. In: Scientific Applications of Current Diving Technology on the US Continental Shelf, NOAA Symposium Series for Undersea Research, Washington, DC, Vol. 2, pp. 191–199.

Reed, J.K., Mikkelson, P.M., 1987. The molluscan community associated with the scleractinian coral *Oculina varicosa*. Bulletin of Marine Science 40 (1), 99–131.

Rinkevich, B., Loya, Y., 1987. Variability in the pattern of sexual reproduction of the coral *Stylophora pistillata* at Eilat, Red Sea: a long term study. Biological Bulletin 173, 335–344.

Sasaki, R., Shepherd, S.A., 1995. Larval dispersal and recruitment of *Haliotis discus hannai* and *Tegula* spp. on Miyagi coasts Japan. Marine Freshwater Research 46 (3), 519–529.

Simpson, C.J., 1985. Mass spawning of scleractinian corals in the Dampier archipelago and the implications for management of coral reefs in Western Australia. Western Australia, Department of Conservation of Environment, Bulletin 244, 35.

Smith, N.P., 1981. An investigation of seasonal upwelling along the Atlantic Coast of Florida. In: Nihoul, J.C. (Ed.), Ecohydrodynamics. Elsevier, New York, pp. 79–98.

Smith, N.P., 1983. Temporal and spatial characteristics of seasonal upwelling along Florida's Atlantic shelf. Journal Physical Oceanography 13 (9), 1709–1715.

Smith, N.P., 1987. Near-bottom cross-shelf heat flux along central Florida's Atlantic shelf break: winter months. Journal Geophysical Research 92, 10845–10852.

Stoddardt, J.A., Black, R., 1985. Cycles of gametogenesis and planulation in the coral *Pocillopora damicornis*. Marine Ecology—Progress Series 23, 153–164.

Szmant-Froelich, A.M., Yevich, P., Pilson, M.E.Q., 1980. Gametogenesis and early development of the temperate coral *Astrangia danae* (Anthozoa: Scleractinia). Biological Bulletin 158, 25–269.

Szmant-Froelich, A.M., Reutter, M., Riggs, L., 1985. Sexual reproduction of *Favia fragrum* (Esper): lunar patterns of gametogenesis, embryogenesis and planulation in Puerto Rico. Bulletin of Marine Science 37, 880–892.

Tranter, P.R.G., Nicholson, D.N., Kitchington, D., 1982. A description of the spawning and post gastrula development of the cool temperate coral *Caryophillia smithii* (Stokes and Broderip). Journal of the Marine Biological Association, UK 62, 845–854.

Yankson, K., 1986. Reproductive cycles of *Cerastoderma glaucum* (Bruguiere) and *C. edule* (L.) with special reference to the effects of the 1981–82 severe winter. Journal of Molluscan Studies 52 (1), 6–14.